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ON SPLITTING OF THE GENUS *NOTOCUPES* (COLEOPTERA: ARCHOSTEMATA): NEW DATA ON MORPHOLOGY AND TAXONOMY

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Summary. *Notocupes* is a speciose genus of Mesozoic Archostemata, currently including 69 species. Due to its distinct morphological heterogeneity and polyphyly it is advised to split *Notocupes* into four genera based on full body imprints: *Notocupes* Ponomarenko, 1964, *Rhabdocupes* Ponomarenko, 1966, *Conexicoxa* Lin, 1986, **stat. resurr.** and *Brachilatus* Strelnikova et Yan, **gen. n**. The genus *Zygadenia* Handlirsch, 1906 is proposed for isolated elytra, morphologically similar to those of four aforementioned genera. *Notocupes patulus* is transferred to *Odontomma* Ren et al., 2006 as *O. patula* (Ponomarenko, 1985), **comb. n.** Individual characters, such as body cuticular tuberculation are discussed in detail as a promising diagnostic feature to separate genera and possibly also species. The expanded diagnoses for five genera and keys to species of these genera are given. New combinations are proposed for thirty-seven species.

Key words: fossil insects, *Notocupes*, *Rhabdocupes*, *Conexicoxa*, *Brachilatus, Zygadenia, Odontomma,* morphology, taxonomy, new genus, new combinations.

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Резюме. *Notocupes* – это самый многочисленный по количеству видов род мезозойских Archostemata, до настоящего времени включающий 69 видов. Из-за его явной морфологической гетерогенности и полифилии рекомендуется разделить *Notocupes* на четыре рода, описанные по отпечаткам полных тел: *Notocupes* Ponomarenko, 1964, *Rhabdocupes* Ponomarenko, 1966, *Conexicoxa* Lin, 1986, **stat. resurr.** и *Brachilatus* Strelnikova et Yan, **gen. n.** Виды, известные только по изолированным надкрыльям и морфологически схожие по строению с четырьмя вышеупомянутыми родами, предлагается поместить в род *Zygadenia* Handlirsch, 1906. Вид *N. patulus* перенесен в род *Odontomma* Ren et al., 2006 как *O. patula* (Ponomarenko, 1985), **comb.n.** Отдельные признаки, такие как кутикулярные бугорки тела, подробно обсуждаются как многообещающие диагностические признаки для разделения родов и, возможно, видов. Даны расширенные диагнозы 5 родов и определительные таблицы включенных в них видов. Для 37 видов предложены новые комбинации.

INTRODUCTION

Nowadays the genus *Notocupes* Ponomarenko, 1964 consists of 69 species described from around 55 localities worldwide from Late Triassic to Late Cretaceous, being the most diverse genus of Mesozoic Archostemata beetles. Previously these species were included in 11 different genera, gradually synonymized with *Notocupes* over the years (Ponomarenko, 2000, 2006; Tan *et al*., 2005; Kirejtshuk *et al*., 2010, 2016, overview in Kirejtshuk, 2020). Character states that contradict each other and often overlap (for example, elytron venation, Figs 1–4) make it difficult not only to compare described species, but also to identify of new findings and integrating them into *Notocupes* taxonomy. Thus, finding hiatuses between *Notocupes* and other Mesozoic Archostemata also become very difficult.

Habitually *Notocupes* is very similar to closely related genera of Archostemata, for example their elytron have similar structure to those of *Rhopalomma* Ashman et al., 2015, *Rhabdocupes* Ponomarenko, 1966, or *Latocupes* Ren et Tan, 2006 (Strelnikova & Yan, 2023). The elytron of these genera have five more or less straight double rows of cells and veins 4 and 5 fused before the elytral apex. It is notable, that, for example, *Rhabdocupes* in origin description (Ponomarenko, 1966) differs from *Notocupes* only in length ratio of basal antennomeres despite this character being rarely preserved or become very susceptible to spatial distortion due to three-dimensional orientation of the structure in host rock matrix or overall tectonic deformation of the imprint (along one or even several axes). Taxonomic relationships between *Rhabdocupes*, *Notocupes* and *Amblomma* are unclear, due to their morphological similarity and lack of hiatuses (Tan *et al*., 2012; Yamamoto, 2017). Due to high morphological variability, many characters states for *Rhabdocupes* could be also found among *Notocupes*, such as rectangular pronotum without protruding anterior angles. Similarly, while *Rhabdocupes* have straight epipleural margin of elytron and in *Rhopalomma* there are gradually curving, *Notocupes* have species with both of this character. Thus, a reevaluation of morphological characters as well as overall *Notocupes* diagnosis rework is needed and an attempt to do this is made in the present paper.

MATERIAL AND METHODS

The species deposited in the Paleontological Institute of the Russian Academy of Sciences (PIN RAS) were reexamined; other taxa are discussed based on their original descriptions.

Observations were made using stereo microscope MBS-10. Photographs were taken with a DFC-420 digital camera attached to a Leica M165C stereo microscope. Software for image acquisition is Leica Application Suite X. Resulting images were compiled with Helicon Focus 5.1.28 software. Line drawings were made using Corel-Draw X8 software. The SEM micrographs were obtained by a scanning electron microscope Tescan Vega3 and microtomography NeoScan N80. Diagrams have been made in Microsoft Excel 2016. Drawing conventions are: solid line – structures outline; dashed line – damaged or indistinct parts; dashed and dotted – folds of cuticular sculpture and cuticular relief.

Detailed methodology of body measurement and elytral description is provided in earlier study (Strelnikova & Yan, 2021).

MORPHOLOGICAL CHARACTERS

Sixty-six morphological characters were codified and used in the reinterpreted diagnoses genera and species descriptions. The list of characters is given below (the bold numbers indicate generic features; the regular numbers are useful when comparing species).

Body coverings sculpture:

1. Tubercles size on different body localities: 0 – identical tubercles all over the body, they do not differ significantly in size (Fig. 29), 1 – two (Fig. 30) (or rarely three, Fig. 31) types of tubercles, larger tubercles are on the apical abdominal sternite and on the depressed localities on the sternites II–IV.

2. Body is covered with small (0.01–0.02 mm in diameter) tubercles: 0 – yes, 1 – no.

3. Body is covered with medium-size (0.02–0.04 mm in diameter) tubercles: 0 – yes, 1 – no.

4. Body is covered with large (0.04–0.07 mm in diameter) tubercles: 0 – yes, 1 – no.

Head:

5. Body to head length ratio: 0 – not more than 5.5, 1 – not less than 5.6.

6. Head form: 0 – rectangular, do not narrowing anteriorly and posteriorly, 1 – diamond-shaped or rounded, narrowing anteriorly and posteriorly, 2 – trapezoidal, narrowing only anteriorly and do not posteriorly.

7. Head length to width ratio (measured without eyes width): 0 – not more than 1, 1 – from 1 to 1.5, 2 – more than 1.5. REMARK. Head width measured without eyes width because, firstly, eyes are not preserved on all species (Figs 34, 37 – *N. caudatus*), secondly, eyes can be located on dorsal side of head (Figs 33, 36 – *Rh. tenuis*), which would affect the width measured together with the eyes.

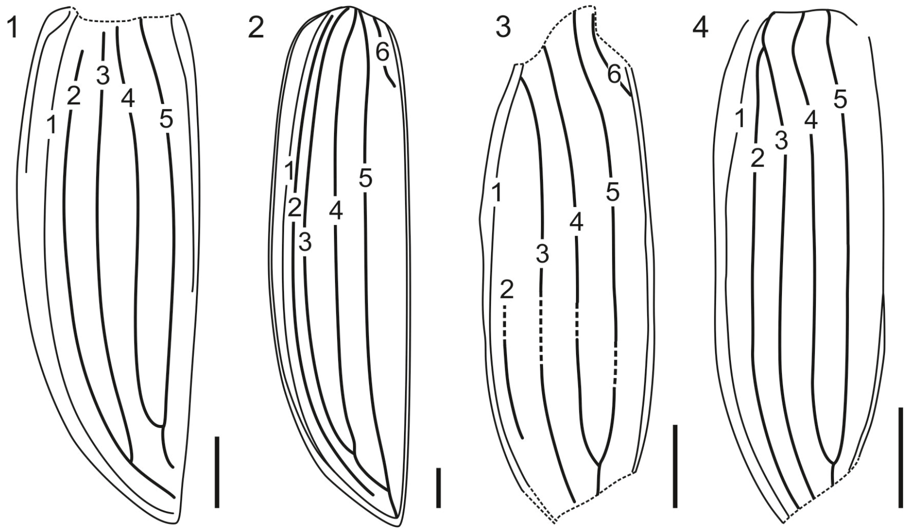
8. Genae protrude forward on the sides of the mandibles: 0 – yes, bending around the mandibles on the sides, 1 – do not protrude.

9. Head width (without eyes width) to eye transverse diameter ratio: 0 – from 2 to 3.5, 1 – from 3.6 to 4.9, 2 – from 5 to 7.

10. Head length in front of the eyes to longitudinal eye diameter ratio: 0 – equal, 1 – longer, 2 – shorter.

11. Head length behind the eyes to longitudinal eye diameter ratio: 0 – equal, 1 – longer, 2 – shorter.

12. Head tubercles form: 0 – P1–P3 merged into a single longitudinal roller (Figs 32, 35), 1 – P1 and P2 merged into a single H-shaped tubercle, P3 isolated or absent (Figs 33, 36), 2 – all tubercles are isolated (Figs 34, 37). REMARK. Head tubercles named after modern *Tetraphalerus bruchi* Heller, 1913 (Beutel *et al*., 2008): P1 – supraantennal protuberance, P2 – supraocular protuberance, P3 – posteromesal protuberance. Manifestations variants of the feature are given approximately and require additional study on materials from other collections.



Figs 1–4. Types of elytral venation. 1 – *Conexicoxa brachicephala* (Ponomarenko, 1994); 2 – schematic drawing of *Zygadenia* spp.; 3 – *Z. liui* Jarzembowski et al., 2015; 4 – *Z. westraliensis* (Riek, 1968). (Figs 1, 2, 4 – redrawing with changes from Ponomarenko, 1994, 2006; Martin, 2010). Scale bar = 1.

Antennae:

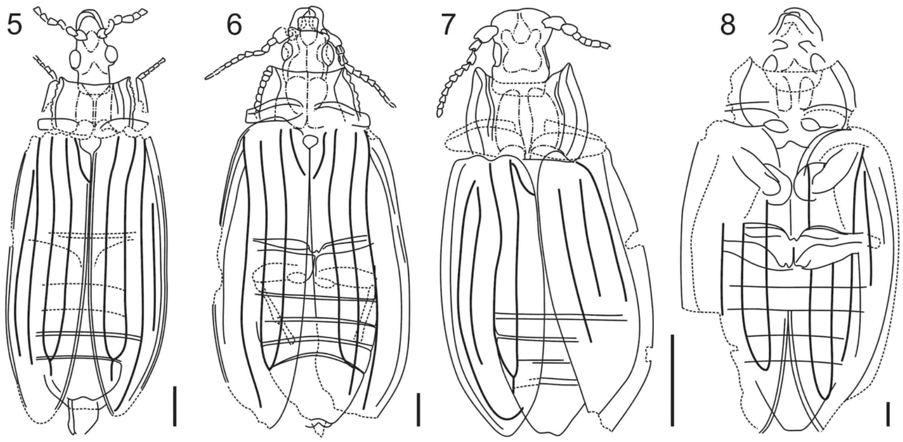
13. Antennae length: 0 – antennae top reaches only the base of the pronotum, 1 – antennae top not reaches the base of the pronotum, 2 – antennae top goes beyond the base of the pronotum.

14. Antennae form: 0 – filiform (Fig. 41), 1 – weakly serrated (Fig. 40), 2 – moniliform (Fig. 39).

15. Antennae localities between the eyes and mandibles: 0 – antennae attached directly in front of the eyes (Figs 34, 39, 41), 1 – antennae attached on the sides of the mandibles get as close to them as possible (Fig. 40), 2 – antennal bases shifted to dorsal side and removed from the eyes and mandibles (Fig. 38).

16. The 2nd to the 3rd antennomere length ratio: 0 – the 3rd antennomere longer than the 2nd (Fig. 40), 1 – equal (Figs 39, 41), 2 – the 2nd antennomere longer than the 3rd (*N. picturatus*).

17. Antennomere 4–11: 0 – successively shortened towards the top (Figs 39–41), 1 – identical in size (*Rh. laticella*, *Rh. rostratus*).



Figs 5–8. Representatives of the four investigated genera. 5 – *Rhabdocupes protensus* (Tan et al., 2006); 6 – *Conexicoxa epicharis* (Tan, Ren et Liu, 2005); 7 – *Notocupes picturatus* Ponomarenko, 1964; 8 – *Brachilatus longicoxa* (Soriano et Martinez-Delclòs, 2006). Scale bar = 1 mm.

Pronotum:

18. Pronotal coloring: 0 – pronotal lateral margin and tubercles dark, 1 – pronotum without dark spot.

19. Pronotal width to length ratio: 0 – not more than 1.6 (Figs 42–45, 47), 1 – not less than 1.7 (Fig. 46).

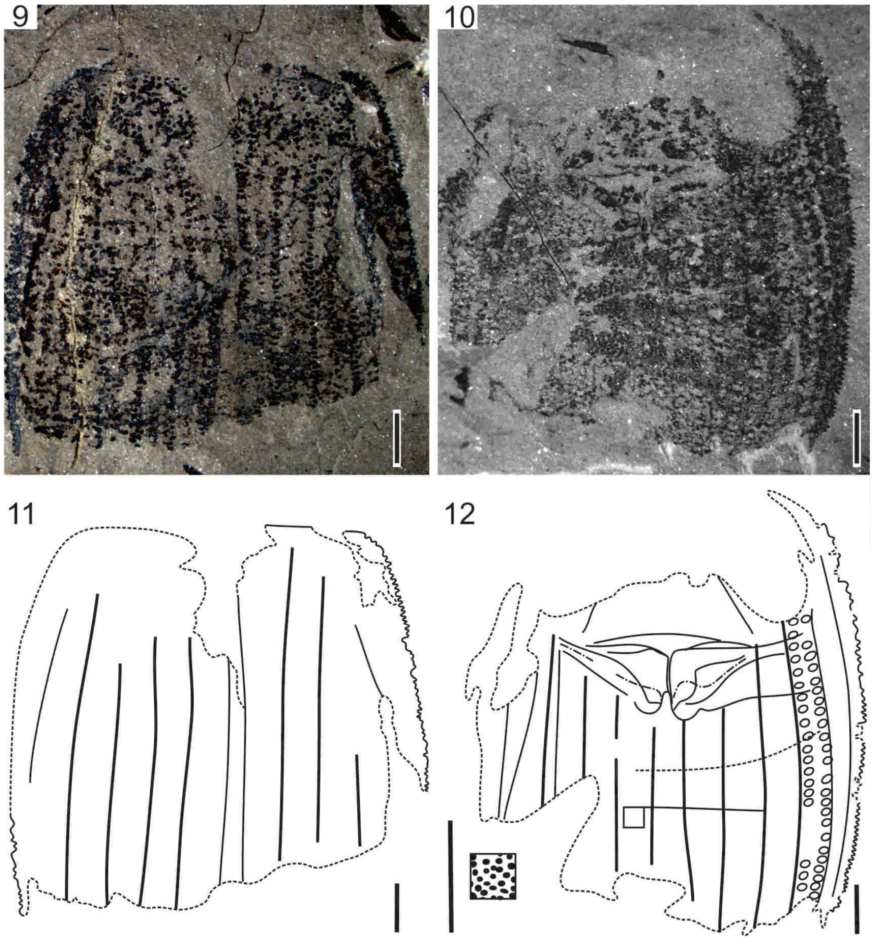
20. Pronotal form: 0 – pronotum rounded, narrowing anteriorly and posteriorly (Figs 7, 8, 42, 43, 45, 47), 1 – pronotum rectangular, do not narrowing anteriorly and posteriorly (Figs 5, 44), 2 – pronotum trapezoidal, narrowing anteriorly, but do not posteriorly (Fig. 6).

21. Pronotal width in the widest part to his width along the anterior margin ratio: 0 – more than 1.5 (Figs 43, 46), 1 – not more than 1.5 (Figs 5, 7, 42, 45, 47). REMARK. Investigational species pronotum can have the most width as along the posterior margin as in his central part, narrowing posteriorly. In this case numeral values pronotal width along the posterior margin to his width along the anterior margin ratio can be similar in species with an almost rectangular pronotum and with a pronotum expanded in the central part. This interpretation is proposed to use the most width of pronotum to his width along the anterior margin ratio regardless of the shape of pronotum.

22. Presence of anterior angles of the pronotum protruding forward: 0 – anterior angles of the pronotum do not or just a little protruding forward not reaching to eyes (Figs 5, 6, 45, 47), 1 – anterior angles of the pronotum strongly protruding forward reaching or even goes beyond the base of eyes (Figs 7, 42, 43, 46).

23. Presence of semicircular concavity on the anterior margin of pronotum: 0 – there is present (Fig. 46), 1 – absent, anterior margin of pronotum straight in his central part (Figs 5, 6, 43, 47).

24. Pronotal posterior margin form: 0 – pronotal posterior margin straight with distinct posterior angles (Fig. 43), 1 – pronotal posterior margin smoothly curved, posterior angles blunted (Figs 45, 47).



Figs 9–12. *Odontomma patula* (Ponomarenko, 1985). 9 – photograph of the print; 10 – photograph of the counterprint; 11 – interpretative linedrawing of the print; 12 – interpretative linedrawing of the counterprint. Cuticular tubercles depicted in a square frame. Scale bar = 1 mm.

25. Form of pronotal lateral margin: 0 – smooth lateral margins (Figs 7, 44–46), 1 – lateral margins dentate (Figs 5, 6, 42, 43, 47).

26. Pronotal disk: 0 – with square or rectangular central protuberance (Figs 5, 45), 1 – with cordate protuberance (Figs 6, 46), 2 – with ovate protuberance (Figs 7, 47). REMARK. Pronotum tubercles form explored only on species from PIN. Manifestation variants of them are given approximately and require additional study on materials from other collections.

27. Pronotal to head width ratio: 0 – not more than 2.4, 1 – more than 2.4.

28. Presence of tubercles between the anterior angles of pronotum: 0 – presence (*N. alienus*), 1 – absent (Figs 42–47).

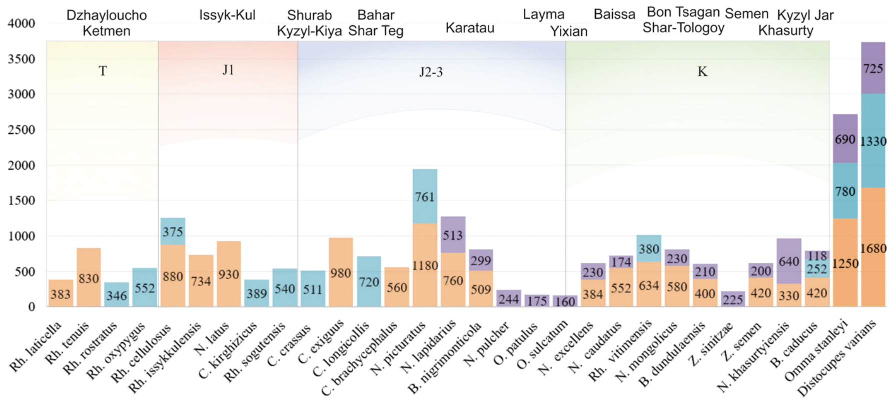


Fig. 13. Size and density of cuticular tubercles in species studied of ancient *Rhabdocupes*, *Conexicoxa*, *Notocupes*, *Brachilatus*, *Odontomma*, *Zygadenia* and some extant *Omma* and *Distocupes*. Tubercles of *Odontomma sulcatum* were examined from photographs in Kirejtshuk (2020). Yellow – Triassic species; Red – Early Jurassic; Blue – Middle to Late Jurassic; Green – Cretaceous. Here and further orange columns represent density of small (0.01–0.02 mm in diameter), blue – density of middle-sized (0.02–0.04 mm in diameter), violet – density of large (0.04–0.07 mm in diameter) tubercles. Names of localities are given above columns.

Prosternum:

29. Notopleural suture: 0 – beveled V-shape in his anterior part from the anterior angles of pronotum to the center, then straight to the posterior margin of prosternum (Figs 43, 45), 1 – straight (Fig. 42), 2 – beveled out at the posterior part (Fig. 44).

30. Pleurosternal suture: 0 – beveled V-shape in his anterior part from the anterior angles of pronotum to the center, then straight to the posterior margin of prosternum (Fig. 46), 1 – extends obliquely towards the procoxae (*C. psilata*, *N. rudis*, *C. stabilis*), 2 – straight (Fig. 42).

31. Propleuron shape: 0 – do not or only slightly narrowing anteriorly (Figs 42, 43), 1 – strongly narrowing anteriorly (Fig. 44).

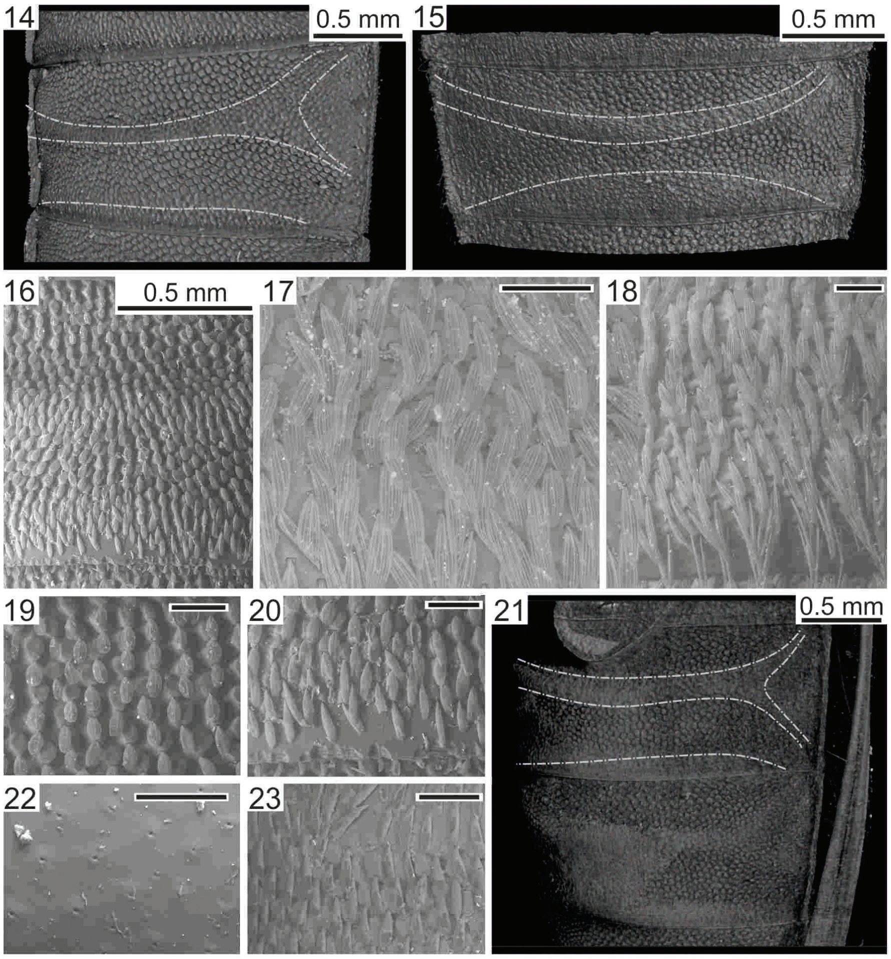
Scutellum:

32. Scutellum form: 0 – triangular, 1 – pentangular.

Elytron:

33. Elytron design: 0 – absent, 1 – design as transverse spots and strips.

34. Elytral length to width ratio – 0 – more than 3.4, 1 – from 2.9 to 3.3, 2 – not more than 2.8.



Figs 14–23. Integuments of extant Archostemata. 14, 16, 19, 20, 22 – *Omma stanleyi* Newman, 1839: 14 – abdominal sternite, tomography image; 16 – SEM–micrography of scales; 19 – SEM–micrograph of wide scales attached to larger tubercles; 20 – SEM–micrograph of narrow scales, attached to middle–sized tubercles; 22 – SEM–micrograph of abdominal sternite; 15, 17, 18 – *Priacma serrata* (LeConte, 1861): 15 – abdominal sternite, tomography image; 17 – SEM–micrograph of scales on large tubercles; 18 – SEM–micrograph of two types of scales and tubercles; 21, 23 – *Distocupes varians* (Lea, 1902): 21 – abdominal sternites, tomography image; 23 – SEM–micrograph of scales on large tubercles. Dashed and dotted lines indicate narrow elevated portions of sternites. Scale bar = 1 mm if not stated otherwise.

35. Elytral common width to pronotal width ratio: 0 – not more than 1.6, 1 – more than 1.6.

36. Elytral base form: 0 – straight (Figs 7, 25), 1 – rounded (Fig. 6).

37. Humerus: 0 – pronounced (Fig. 8), 2 – sloping, not pronounced (Figs 5–7, 25–28).

38. Epipleural rim form: 0 – smoothly rounded throughout (Figs 6–7, 27–28), 1 – more or less straight in anterior part, obliquely oblique in posterior third (Figs 5, 8, 25–26).

39. Epipleural rim structure: 0 – epipleural rim smooth (Figs 5–7, 25–28), 1 – epipleural rim dentate at least in the basal third (*N. excellens*).

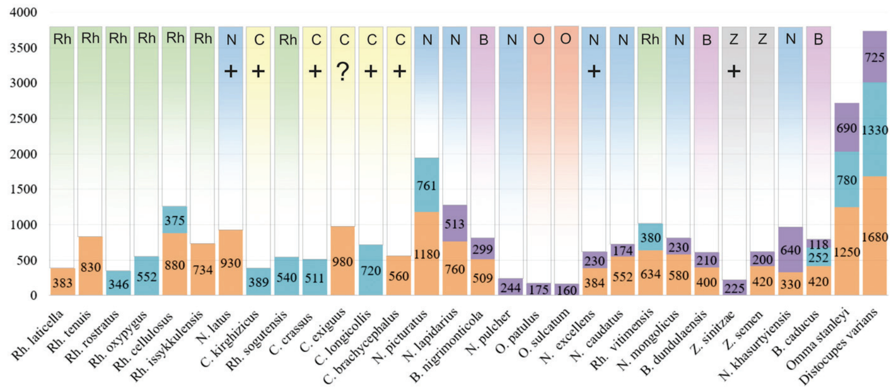


Fig. 24. Tubercles size-density variability among different Archostemata genera. B (violet) – *Brachilatus*; C (yellow) – *Conexicoxa*; N (blue) – *Notocupes*; O (red) – *Odontomma*; Rh (green) – *Rhabdocupes*; Z (grey) – *Zygadenia*. Species with veins 2 and 3 merging before reaching elytron apex are marked with “+”, or with “?” if this character is unclear.

40. Anterior to posterior epipleural width ratio: 0 – not more than 4, epipleuron almost not or smoothly a little narrowing posteriorly (Figs 5–7), 1 – not less than 4, epipleuron smoothly or abruptly strongly narrowing (Fig. 8).

41. Elytral to epipleural maximum width ratio: 0 – not more than 9, epipleuron wide (Figs 8, 25–28), 1 – more than 9, epipleuron narrow (Fig. 7).

42. Characteristics of the narrowing of the epipleura: 0 – almost do not or smoothly narrowing throughout (Figs 5–7, 27–28), 1 – abruptly strong narrowing in anterior half of elytral length (Figs 8, 25–26).

43. Elytron apex: 0 – blunted (Figs 5–7), 1 – acute (Figs 25–26).

44. Intercalary between the veins are at least in some fields: 0 – pronounced (Fig. 52), 1 – absent (Figs 48–51).

45. Merge side of two main veins 4 and 5 closest to the suture margin: 0 – three-four cells before elytron apex (Figs 25, 26), 1 – another (Figs 27, 28).

46. Veins 2 and 3 apart reaching elytral apex: 0 – yes (Figs 25, 26), 1 – not, merging before reaching elytral apex (Figs 27, 28).

47. Veins 2 and 3 forms: 0 – straight almost all the way, only slightly curving at the ends (Figs 5, 8, 25–26), 1 – veins 2 and 3 curved (Figs 6–7, 27–28).

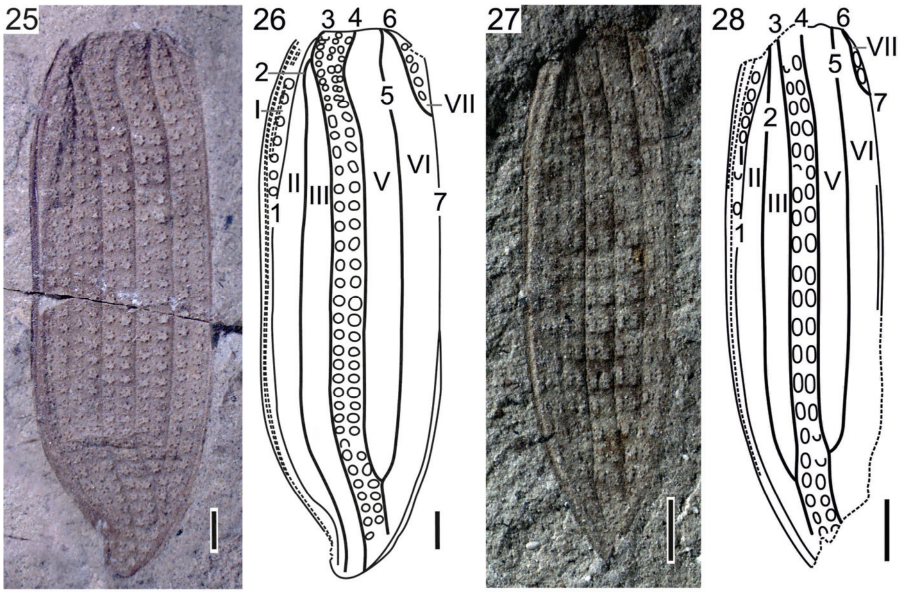
48. Sutural vein: 0 – absent or present, but separates only a narrow field without cells, 1 – present and separate from the sutural margin two cells (Figs 27, 28), 2 – present and separate

from the sutural margin three and more cells (Figs 25, 26). REMARK. In the different papers this vein named A2 (Crowson, 1962) or A3 (Jarzembowski *et al*., 2015).

49. Longitudinal veins have tubercles along the entire length: 0 – yes (*Z. giebeli*, *Z. handlirshi*), 1 – no.

50. Y-shaped veinlets make a zig-zag vein-like structure: 0 – yes (Fig. 50), 1 – no (Figs 48, 49, 51, 52).

51. Elytral cells form: 0 – rounded (Fig. 48) or ovate (Figs 49, 52), 1 – square (Fig. 50) or multifaceted (Fig. 51).



Figs 25–28. Elytron venation types of five investigated genera of Archostemata. 25, 26 – *Zygadenia alexrasnitsyni* Strelnikova et Yan, 2021: 25 – photograph; 26 – interpretative linedrawing; 27, 28 – *Notocupes elegans* Ponomarenko, 1994: 27 – photograph; 28 – interpretative linedrawing. Elytral fields marked with Roman numerals, veins – with Arabic. Scale bar = 1 mm.

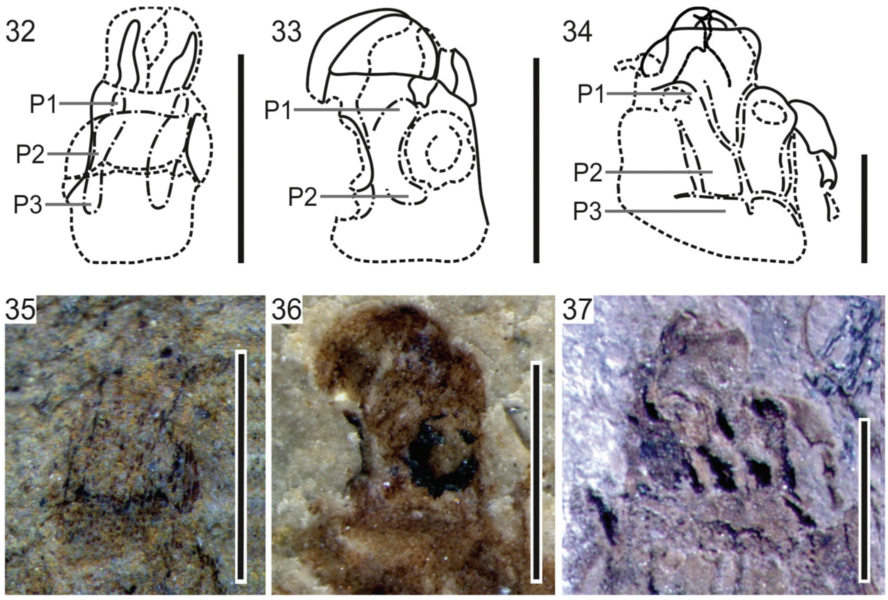
Figs 29–31. Characteristic of cuticular coverings five investigated genera of Archostemata. 29 – *Rhabdocupes oxypygus*, covered with one type of cuticular tubercles; 30 – *Notocupes caudatus*, covered with two types of cuticular tubercles; 31 – *Brachilatus caducus*, covered with three types of cuticular tubercles. Scale bar = 1 mm.

52. Elytral cells size: 0 – cells small, occupy less than half the distance between the veins (Figs 51, 52), 1 – cells medium-sized, occupy half or more the distance between the veins and clearly do not reach the fields edges (Fig. 49), 2 – cells large, occupy more than half the distance between the vein and almost reach the fields edges (Figs 48, 50). REMARK. Earlier in descriptions (Ponomarenko, 1969; Soriano & Delclòs, 2006; Martin, 2010; Ponomarenko *et al*., 2014) often met subjective estimates of cell size large/medium-sized/small. In this matrix proposed more accurate wording.

53. Number of cells in elytral row in the field IV: 0 – 20–25, 1 – 26–29, 2 – 30 and more.

54. Cells in epipleuron: 0 – absent, 1 – present.

55. Difference of cells in epipleuron and in elytral disk: 0 – differ in size, 1 – no.



Figs 32–37. Head tubercles located and form. 32–34 – linedrawings: 32 – *Rhabdocupes laticella*; 33 – *Rhabdocupes tenuis*; 34 – *Notocupes caudatus*; 35–37 – head photographs: 35 – *Rhabdocupes laticella*; 36 – *Rhabdocupes tenuis*; 37 – *Notocupes caudatus*. Abbreviations: P1 – supraantennal protuberance; P2 – supraocular protuberance; P3 – posteromesal protuberance. Scale bar = 1 mm.

Metatorax:

56. Metaventrite width along the posterior margin to the along anterior margin ratio: 0 – 1.6-2.4 (Figs 53, 55, 56), 1 – 2.5–3 (Fig. 54).

57. Metaventrite width along the posterior margin to his length ratio: 0 – not more than 1.1 (Fig. 56), 1 – from 1.2 to 1.9 (Figs 54, 55), 2 – not less than 2 (Fig. 53).

58. Location of paracoxal suture: 0 – paracoxal suture reaches the posterior angles of metaventrite (Figs 53, 54, 56), 1 – paracoxal suture is interrupted before reaching the posterior angles of metaventrite (Fig. 55).

Abdomen:

59. Form and location of depressions on the abdominal sternites: 0 – depressions are along the anterior margin of sternites II–IV (Fig. 30), 1 – depressions are along the anterior and posterior margins (Fig. 29), 2 – depressions along the anterior margin and additional triangular or ovate lateral depressions (Fig. 31).

60. Narrowing of the abdomen to the base: 0 – present (Figs 57), 1 – absent (Figs 58, 59).

61. Narrowing of the abdomen to the apex: 0 – from the third abdominal sternite (Figs 57, 59, 60), 2 – from the fourth or fifth abdominal sternite (Fig. 58).

62. Form of the abdominal apex: 0 – acute (Figs 57, 58), 1 – blunted, medially with a fossa (Figs 59, 60). REMARK. In some articles, one can find a feature "the sternite length to the it's elevated part length ratio" (Ponomarenko, 1968: 121–122). It is almost impossible to reliably measure this interval due to taphonomic features. Therefore, it is not considered in this matrix.

63. The apical abdominal sternite width to length ratio: 0 – not more than 1.5 (Figs 58, 59), 1 – more than 1.5 (Figs 57, 60).

64. The apical abdominal sternite to penultimate one length ratio: 0 – not more than 2.2 (Fig. 59), 1 – not less than 3 (Fig. 60), 2 – from 2.3 to 2.9 (Figs 57, 58).

Procoxae:

65. Procoxal location: 0 – located along the pronotal posterior margin, 1 – removed from the pronotal posterior margin (*Rh. laticella*, *Rh. tenuis*).

Metacoxae:

66. The first abdominal sternite to metacoxal length ratio: 0 – shorter than 2, metacoxae less than half as long as sternite I, 1 – not shorter than 2, metacoxae is half or more than the length of the first abdominal sternite.

TAXONOMY

Order Coleoptera

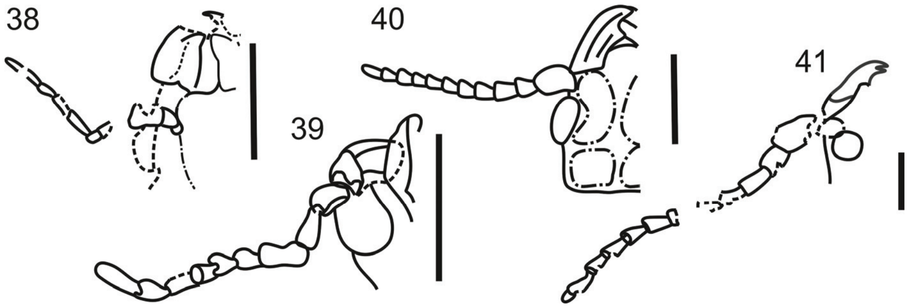
Suborder Archostemata

REMARKS. Position of the fossil genus *Notocupes* and related genera within families of suborder Archostemata is still uncertain. There are two points of view regarding the taxonomic status of the family Ommatidae: treating it as a subfamily of Cupedidae (Kirejtshuk *et al*., 2016; Jarzembowski *et al*., 2016, 2017, 2019; Kirejtshuk, 2020, 2021) and as a separate family (Lawrence, 1999; Tan *et al*., 2006, 2012; Tihelka *et al*., 2019; Jiang *et al*., 2020; Strelnikova & Yan, 2021, 2023). There is also a suggestion to placed *Notocupes* and related genera into a separate family Notocupedidae (Li *et al*., 2023a, b). Thus, *Notocupes* should be used without specifying the family (Li *et al*., 2023a) until clear diagnoses for the families discussed that can be applied to fossil material will be formulated.

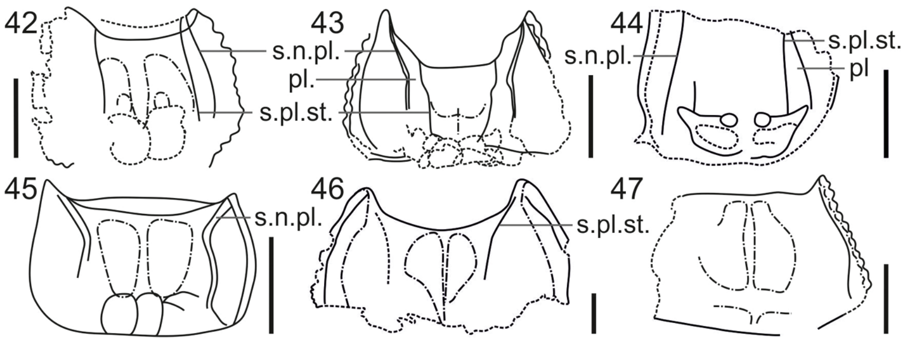
Genus *Rhabdocupes* Ponomarenko, 1966

Type species: *Rhabdocupes longus* Ponomarenko, 1966.

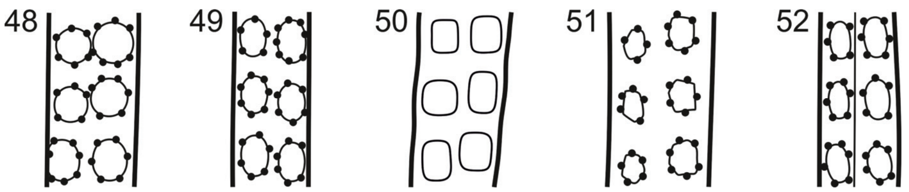
DIAGNOSIS. Beetles with narrow bodies, body length to width ratio distinctly more than 2. Integument with tubercles of small or medium-size, uniform in shape (Fig. 29). Head rectangular or trapezoid. Head length in front of eyes is equal or slightly exceed eye longitudinal diameter; head width to eye transverse diameter ratio



Figs 38–41. Antennae morphology. 38 – filiform of *Notocupes pulcher*; 39 – moniliform of *Notocupes excellens*; 40 – weakly serrated of *Rhabdocupes minisculus*; 41 – filiform of *Brachilatus nigrimonticola*. Scale bar = 1 mm.



Figs 42–47. Pronotal and prosternal morphology. 42 – *Notocupes pulcher*; 43 – *Notocupes excellens*; 44 – *Rhabdocupes vitimensis*; 45 – *Notocupes elegans*; 46 – *Brachilatus nigrimonticola*; 47 – *Notocupes caudatus*. Abbreviations: pl – propleuron; s.n.pl. – notopleural suture; s.pl.st. – pleurosternal suture. Scale bar = 1 mm.



Figs 48–52. Form and size of elytral cells. 48 – large round cells of *Rhabdocupes vitimensis*; 49 – medium-sized ovate cells of *Conexicoxa kirghizica*; 50 – square large cells of *Notocupes excellens*; 51 – multifaceted small cells of *Notocupes dundulaensis*; 52 – small ovate cells with pronounced intercalary of *Rhabdocupes tenuis*.

is 4–5. Pronotum rectangular, not narrowing or only slightly narrowing anteriorly, not narrowing posteriorly; pronotal anterior margin weakly concave, its anterior angles not protruding forward or protruding only slightly; pronotal disc with rectangular median protuberance. Elytral epipleural margin straight, veins 2 and 3 follow epipleuron, form straight parallel rows, not merging together before reaching elytral apex. Epipleuron almost not narrowing towards the apex or narrowing slightly and gradually at elytron basal half (distinctly narrowing only in *Rh. minisculus*). Elytral cells are round or oval-shaped.

COMPOSITION. This genus consists of 15 species from Triassic of Kyrgyzstan and Kazakhstan, Jurassic of Kyrgyzstan, Jurassic-Cretaceous of China and Lower Cretaceous of Russia, namely *Rh. longus* Ponomarenko, 1966, *Rh. baculatus* Ponomarenko, 1969, *Rh. cellulosus* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *Rh. dischides* (Zhang, 1986), **comb. n.** [*Notocupes*], *Rh. issykkulensis* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *Rh. laticella* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *Rh. lentus* (Ren, 1995), **comb. n.** [*Tetraphalerus, Notocupes*], *Rh. minisculus* (Tan et al., 2006), **comb. n.** [*Amblomma, Notocupes*], *Rh. minor* Ponomarenko, 1966, *Rh. oxypygus* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *Rh. protensus* (Tan et al., 2006), **comb. n.** [*Amblomma, Notocupes*], *Rh. rostratus* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *Rh. sogutensis* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *Rh. tenuis* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *Rh. vitimensis* (Ponomarenko, 1966), **comb. n.** [*Notocupes*].

Key to species of the genus *Rhabdocupes*

(*Rh. dischides* not included in the key due to lack of photographs and linedrawings detailed enough to identify its diagnostic characters)

1. Large elytron, length 11.7; about 47cells in one row ……………….......… ***Rh. baculatus***
– Small or medium-sized elytron, length from 2 to 7.5, number of cells in one row not exceeding 30 ………………………………........…………………….………………… 2
2. Small beetle, elytron`s length 4.5–6, elytron with large cells (cells occupy more than half the distance between the vein and almost reaches the field`s edges) …..…….. ***Rh. minor***
– Beetles from small to large, elytron not shorter than 5, if shorter than 6, then it has small cells (cells occupy less than half the distance between veins) ……………..…..…….… 3
3. Metaventrite almost square-shaped ……………………………………...…..………... 4
– Metaventrite`s width 1.3–2 exceeds its length ………………………………..……….. 8
4. Epipleuron narrow, elytron`s width to epipleuron width ratio is no less than 9 ....…. 5
– Epipleuron wide, elytron`s width to epipleuron width ratio is less than 9 ………….....… 6
5. 23–24 elytral cells in one row ……………………………………......….… ***Rh. laticella***
– About 26 elytral cells in one row ………………………………...…...……... ***Rh. longus***
6. 25–27 elytral cells in one row; paracoxal suture laterally reaching posterior angles of metaventrite; apical abdominal sternite 2.5 times longer than penultimate one …..…..… ………………………………………………………………….......….. ***Rh. sogutensis***
– 30–31 elytral cells in one row; paracoxal suture laterally not reaching posterior angles of metaventrite; apical abdominal sternite less than 2.5 times longer than penultimate one ……………………………………………………………...……...…….……… 7

7. Body covered with medium-sized tubercles (0.02–0.04 mm in diameter), density is 346 tb/mm² …………………………………………………………........… ***Rh. rostratus***
– Body covered with small tubercles (0.01–0.02 mm in diameter), density is 734 tb/mm² … ………………………………………………………………….…… ***Rh. issykkulensis***
8. Distinct intercalary veins present between main ones, their thickness is similar, 30 elytral cells in one row …………………………………………..…………………………… 9
– Main veins clearly thicker than intercalary ones, 23–27 elytral cells in one row …..…..… 10
9. Body covered with small tubercles (0.01–0.02 mm in diameter); epipleuron of medium width, 8 times narrower than elytron ……………………………………..… ***Rh. tenuis***
– Body covered with two types (small and medium-size) of tubercles; epipleuron wide, 4.4 times narrower than elytron ………………………………………….… ***Rh. cellulosus***
10. Abdominal apex blunt ………………………………………………….….....………….. 11
– Abdominal apex acute ....………………………………………...……….….… 12
11. 27 medium-sized elytral cells in one row (cells occupy space not less than half distance between veins, but distinctly not reaching outer margins of respective fields, Fig. 48); apical abdominal sternite less than 2.9 times longer than penultimate one …………….. ………………………………………………………….……….…..... ***Rh. vitimensis***
– About 24 small elytral cells in one row (cells occupy space less than half distance between veins, Fig. 51); apical abdominal sternite less than 2.1 times longer than penultimate one (Fig. 5) ……………………………………………………….……….…… ***Rh. protensus***
12. About 32 elytral cells in one row; length and width of apical abdominal sternite are equal ………………………………………………………………….…….….… ***Rh. oxypygus***
– 23–28 elytral cells in one row; width of apical abdominal sternite 1.4–1.6 times exceeds width ……………………………………………………………………………... 13
13. 26–28 elytral cells in one row ……………………….……….……..…. ***Rh. lentus***
– About 23 elytral cells in one row ...………………………….…………….….. ***Rh. miniscului***

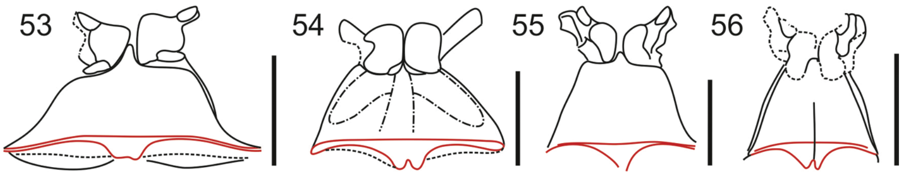
Genus *Conexicoxa* Lin, 1986, stat. resurr.

Type species: *Conexicoxa homora* Lin, 1986.

DIAGNOSIS. Beetles with narrow (body length to width ratio is 2.7–2.9) or wide body (body length to width ratio is 1.7–2.2). Integument with single type of medium-size (0.02–0.04 mm in diameter), or, less common, small (0.01–0.02 mm in diameter) tubercles (Fig. 29). Antennae filiform or weakly serrated (*C. denticollis*). Pronotum trapezoid, pronotal disc bears mesal cordate protuberance. Elytral humerus sloping, not protruding laterally (except *C. psilata*), epipleural margin gradually curving along its length, epipleuron wide (except in *C. siniestri* and *C. exigua* which have narrow epipleuron), gradually, weakly narrowing or almost not narrowing apically, elytral veins 2 and 3 curving towards sutural margin, not forming straight parallel rows, could merge together before reaching elytral apex. Abdomen not narrowing basally (Fig. 58).

REMARKS. *Conexicoxa* was previously treated as a junior synonym of *Notocupes* (Ponomarenko *et al*., 2012), but restored as separated genus in the present study for *Notocupes* species with trapezoid pronotum and curved epipleural margin.

COMPOSITION. This genus consists of 17 species from Jurassic of Germany, Mongolia, China and Kyrgyzstan, Upper Jurassic-Lower Cretaceous of China, Lower Cretaceous of Spain and Russia, namely *C. homora* Lin, 1986, *C. brachicephala* (Ponomarenko, 1994), **comb. n.** [*Notocupes*], *C. crassa* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *C. denticollis* (Jiang et al., 2020), **comb. n.** [*Notocupes, Echinocups*], *C. epicharis* (Tan, Ren et Liu, 2005), **comb. n.** [*Amblomma, Notocupes*], *C. eumeura* (Tan et al., 2006), **comb. n.** [*Amblomma, Notocupes*], *C. exigua* (Ponomarenko, 1994), **comb. n.** [*Notocupes*], *C. jurassica* (Hong, 1983), **comb. n.** [*Chengdecupes, Notocupes*], *C. khetanensis* (Ponomarenko, 1993), **comb. n.** [*Notocupes*], *C. kirghizica* (Ponomarenko, 1969), **comb. n.** [*Notocupes*], *C. longicollis* (Ponomarenko, 1994), **comb. n.** [*Notocupes*], *C. martinclosas* (Soriano et Martinez-Delclòs, 2006), **comb. n.** [*Zygadenia, Notocupes*], *C. porrecta* (Tan et al., 2006), **comb. n.** [*Amblomma, Notocupes*], *C. psilata* (Tan, Ren et Liu, 2005), **comb. n.** [*Amblomma, Notocupes*], *C. siniestri* (Soriano et Martinez-Delclòs, 2006), **comb. n.** [*Zygadenia, Notocupes*], *C. stabilis* (Tan, Ren et Liu, 2005), **comb. n.** [*Amblomma, Notocupes*], *C. tripartita* (Oppenheim, 1888), **comb. n.** [*Procarabus, Notocupes*].



Figs 53–56. Metaventrite structure. 53 – *Conexicoxa crassa*; 54 – *Notocupes excellens*; 55 – *Rhabdocupes oxypygus*; 56 – *Rhabdocupes issykkulensis*. Red indicates paracoxal suture and posterior margin of metaventrite. Scale bar = 1 mm.

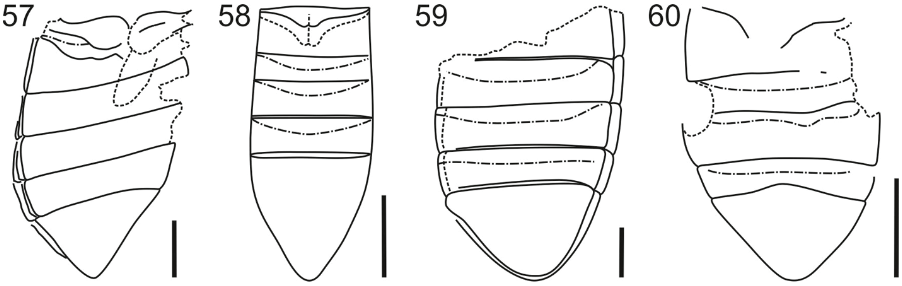
Key to species of the genus *Conexicoxa*

(*C. crassa* and C. *jurassica* were excluded from the identification key due to insufficient information about their diagnostic characters)

1. Beetles with narrow body and narrow pronotum (body length to width ratio 2.7–2.9; pronotum width to length ratio 1.3–1.6) ………………………………….……......………….... 2
– Beetles with wide body and pronotum (body length to width ratio 1.7–2.1, pronotum width to length ratio 1.7–2.2) ....…………………………………………………...…..……………… 6
2. Abdomen narrowing apically starting from the 3rd sternite, apical sternite 2–2.7 times longer than penultimate one; elytral cells usually of medium-size, cells occupy half distance or more between the veins and clearly do not reach the fields edges (Fig. 49), number of elytral cells in one row differs .……………….................…………………..……………... 3
– Abdomen narrowing apically starting from the 4th or the 5th sternite, apical sternite 2.6–2.9 times longer than penultimate one; elytral cells large, occupy more than half the distance between the vein and almost reach the fields edges (Figs 48, 50), often located close to fields sides; usually 26 cells per one elytral row ...……………….………………..…. 5
3. Apical abdominal sternite 2–2.2 times longer than penultimate one ......…… **C. *kirghizica***
– Apical abdominal sternite 2.5–2.7 times longer than penultimate one ...……..…………..... 4

4. Apical abdominal sternite 2.5 times longer than penultimate one, abdominal apex blunt ….
……………………………………………………………………...……….. *C. homora*
– Apical abdominal sternite 2.7 times longer than penultimate one, abdominal apex acute ...
..………………………………………………………………….……… *C. tripartita*
5. Head 2.8 times narrower than pronotum. Body covered with small tubercles, not larger than 0.02 mm in diameter, density is 980 tb/mm^2. Elytral length to width ratio 2.8–3.1. Abdomen narrowing posteriorly from the base of the 4th sternite, apical sternite`s width to length ratio 2.1 ...……………………………………….…………………… *C. exigua*
– Head 2.3 times narrower than pronotum. Body covered with medium-sized tubercles from 0.02 mm to 0.04 in diameter, density is 720 tb/mm^2. Elytral length to width ratio 4. Abdomen narrowing posteriorly from the base of the 5th sternite, apical sternite`s width equal to length (Fig. 58) ....…………………………………………….………… *C. longicollis*

57 58 59 60



Figs 57–60. Abdomen morphology. 57 – *Rhabdocupes rostratus*; 58 – *Conexicoxa longicollis*; 59 – *Brachilatus caducus*; 60 – *Notocupes lapidarius*. Scale bar = 1 mm.

6. Head narrowing only anteriorly. Elytron 1.4–1.6 times wider than pronotum …………..… 7
– Head not narrowing (except C. *psilata*). Elytron may be wider than pronotum by more than 1.6 …………………………………………………………………………….…….... 11
7. Body wide, pronotum and elytron both wide (Fig. 1), body length to width ratio 1.7. Elytron not less than 1.6 times wider than pronotum ………………..... *C. brachicephala*
– Beetle with narrower body, body length to width ratio 2–2.2. Elytron no more than 1.6 times wider than pronotum ……………….……………………………………….……..…. 8
8. Epipleuron narrow, 9 times narrower than elytron. Abdominal apical sternite 3 times longer than penultimate one ….........……………………………………………….…. *C. siniestri*
– Epipleuron wide, 5–6 times narrower than elytron. Abdominal apical sternite 2.1–2.5 times longer than penultimate one ……………………………………………………………… 9
9. Pronotum and elytron strongly dentate laterally; about 21 cells in elytral row …………….
……………………………………………………………………………. *C. denticollis*
– Pronotum and elytron laterally do not dentate, no less than 25 elytral cells in one row 10
10. In one elytral row 25 cells ………………………………………….……. *C. martinclosas*
– In one elytral row 30 cells ………………………………………….…...….. *C. khetanensis*
11. Body elongated, length to width ratio 2.1, pronotal width to length ratio 1.7 (Fig. 6) ...…
…………………………………………………………………….……………. *C. epicharis*
– Body is wider, length to width ratio 1.8, pronotal width to length ratio 1.9–2.2 ……..… 12
12. Body length to width ratio 2, 28 cells in one elytral row ……………………..….… *C. stabilis*
– Body length to width ratio 1.8, 25–26 cells in one elytral row ………………….……… 13

13. Elytral cells without maculae. Apical abdominal sternite 3 times longer than penultimate one ………………………………………………………………………….……….. ***C. psilata***
– Elytral cells with 3–4 maculae. Apical abdominal sternite 3.5–4 times longer than penultimate one ..……………………………………………………………………..… 14
14. Apical abdominal sternite 3.5 times longer than penultimate one ....……… ***C. porrecta***
– Apical abdominal sternite 4 times longer than penultimate one ….…………... ***C. eumeura***

Genus *Notocupes* Ponomarenko, 1964

Notocupes Ponomarenko, 1964: 61, fig. 5.

Sinocupes Lin, 1976: 113 (type species: *Sinocupes validus* Lin, 1976); Ponomarenko, 2006: 90; Kirejtshuk *et al*., 2010: 792.

Forticupes Hong et Wang, 1990: 105 (type species: *Forticupes laiyangensis* Hong, 1990); Ponomarenko, 2006: 90.

Picticupes Hong et Wang, 1990: 107 (type species: *Picticupes tuanwangensis* Hong, 1990); Ponomarenko, 2006: 90.

Ovatocupes Tan et Ren, 2006: 225 (type species: *Ovatocupes alienus* Tan et Ren, 2006); Kirejtshuk *et al*., 2010: 788.

Type species: *Notocupes picturatus* Ponomarenko, 1964.

DIAGNOSIS. Beetles with narrow body; body length to width ratio usually notably greater than 2, no less than 1.8. Antennae filiform, sometimes weakly serrated or moniliform (Figs 38–41). Pronotum with rounded sides, maximum width at midlength; anterior margins are at least slightly protruding forward (usually rather distinctly); pronotal disc with rounded protuberance. Epipleural margin gradually curving. Humerus not protruding anterolaterally, rounded. Epipleuron often wide, abruptly narrowing at elytron base; rarely narrow, almost not narrowing towards elytral apex, only *N. caudatus* and *N. daohugouensis* have wide and almost not narrowing epipleuron. Pronotal sides and/or elytron could be dentate at basal third. Veins 2 and 3 curving, not forming parallel rows, could merge before reaching elytral apex (Fig. 1).

COMPOSITION. The genus consists of 28 species from Jurassic of Germany, Kazakhstan, Kyrgyzstan, China and Lower Cretaceous of China, Mongolia, Spain and Russia, namely *N. reticulatus* (Oppenheim, 1888) [*Procarabus*], *N. alienus* (Tan et Ren, 2006) [*Ovatocupes*], *N. baojiatunensis* (Hong, 1992) [*Chengdecupes*], *N. caudatus* Ponomarenko, 1966, *N. cyclodontus* (Tan et al., 2006) [*Amblomma*], *N. daohugouensis* Li et Cai, 2023*, N. diazromerali* (Soriano et Delclòs, 2006) [*Zygadenia*], *N. elegans* Ponomarenko, 1994, *N. excellens* Ponomarenko, 1966, *N. kezuoensis* (Hong, 1987) [*Chengdecupes*], *N. khasurtyiensis* Strelnikova, 2019, *N. laetus* Lin, 1976, *N. laiyangensis* (Hong, 1990) [*Forticupes*], *N. lapidarius* Ponomarenko, 1968, *N. latus* Ponomarenko, 1969, *N. lini* Ponomarenko et al., 2012, *N. ludongensis* Wang et Liu, 1996, *N. mongolicus* Ponomarenko, 1994, *N. neli* Tihelka et al., 2019 [*Echinocups*], *N. ohmkuhnlei* Jarzembowski et al., 2019 [*Echinocups*], *N. picturatus* Ponomarenko, 1964, *N. pingi* Ponomarenko et Ren, 2010, *N. pulcher*

Ponomarenko, 1968, *N. robustus* Li et Cai, 2023, *N. rudis* (Tan, Ren et Liu, 2005) [*Amblomma*], *N. shiluoensis* (Hong, 1984) [*Chengdecupes*], *N. tuanwangensis* (Hong, 1990) [*Picticupes*], *N. validus* (Lin, 1976) [*Sinocupes*].

Indeterminate species of *Notocupes* were reported from the Middle Triassic of Germany, the Lower and Upper Jurassic of Poland and China, the Jurassic-Cretaceous deposits of Russia and the Lower Cretaceous of England.

REMARKS. Recent study by Li *et al*. (2023a) have several characters in diagnosis, that should be clarified: among the representatives of the genus there are species with length of their head exceeds width (e.g. *N. elegans* and *N. khasurtyiensis*), the head may not be narrowing posteriorly and not form a neck-like constriction (Figs 7, 33, 34, 36, 37, 40), antennas can be not only serrated, but also filiform or moniliform (Figs 38–41). Prosternal intercoxal process is clearly visible on Chinese material, but absent on species from PIN (except *N. laticella*). Thus, this character is absent in present diagnosis, moreover, *N. laticella* have prosternal intercoxal process overlapping contiguous procoxae (Strelnikova &Yan, 2023, fig. 2B), whereas Chinese species have procoxae separated by it. Finally, the epipleuron does not always have cells (e.g. cells are absent in *N. mongolicus*, *N. latus*, *N. picturatus*, *N. excellence*, *N. lapidarius etc*.). *Notocupes trachylaenus* mentioned in Strelnikova & Yan (2021, 2023) was mistakenly attributed to *Notocupes*. This species was previously restored within genus *Lupicupes* Ren, 1995 and its transfer to *Notocupes* was refuted (Kirejtshuk *et al*., 2016).

Key to species of the genus *Notocupes*

(*N. baojiatunensis*, *N. kezuoensis*, *N. laetus, N. laiyangensis*, *N. lini*, *N. ludongensis, N. neli*, *N. ohmkuhnlei*, *N. reticulatus*, *N. shiluoensis*, *N. tuanwangensis* and *N. validus* does not include in a key due to lack of observable diagnostic characters in published sources).

1. Sides of pronotum and/or elytron are dentate at basal third of their length 2
– Pronotum and elytron without denticles 11
2. Abdominal sternites have depressions along their anterior margins and paired triangular lateral depressions. Body covered with two types of tubercles: small and large. Abdomen weakly narrowing basally (except in *N. latus*, which has only small tubercles and has abdomen not narrowing basally) 3
– There are no paired triangular depressions on abdominal sternites. Body covered with uniform tubercles. Abdomen not narrowing basally 8
3. Body covered with single type small (0.01–0.02 mm in diameter) tubercles, abdomen not narrowing basally .... ***N. latus***
– Body has two types of tubercles: small (0.01–0.02 mm in diameter) and large (0.04–0.06 mm in diameter), abdomen slightly narrowing basally 4
4. Pronotal width to length ratio more than 2; metaventrite`s width is equal to its length ....……………………………………………………………………….. ***N. khasurtyiensis***
– Pronotal width to length ratio less than 2; metaventrite`s width to length ratio 1.5–1.8 5
5. Epipleuron without cells, more than 10 times narrower than elytra ....……..…. ***N. excellens***
– Epipleuron with cells, less than 10 times narrower than elytra ....……………….………... 6
6. Epipleuron strongly narrows at basal third, 4 times narrower than its average width ....…………………………………………………………………………... ***N. mongolicus***
– Epipleuron gradually narrows at basal third, 1.3 times narrower than its average width 7

7. Epipleuron narrow, 8.5 times narrower than elytron, the apical abdominal sternite to penultimate one length ratio is 3.1 .... ***N. caudatus***
– Epipleuron wide, 5.9 times narrower than elytron, the apical abdominal sternite to penultimate one length ratio is 2.4 .... ***N. daohugouensis***
8. Antennal bases shifted to dorsal side (Fig. 38) .... ***N. pulcher***
– Antennae attached laterally in front of eyes ....…………………………………………..... 9
9. Pronotum and basal half of elytron`s epipleural margin with distinct denticles. One elytral cell has about 2–3 maculae .... ***N. cyclodontus***
– Basal half of elytron`s epipleural margin not dentate; pronotum laterally dentate. One elytral cell has no less than 3 maculae ……………………………………….……... 10
10. Pronotum laterally slightly dentate, one elytral cell has 3–4 maculae .... ***N. rudis***
– Pronotum laterally strongly dentate, one elytral cell has 5–8 maculae .... ***N. robustus***
11. Head rounded; anterior margin of prosternum have two denticles .... ***N. alienus***
– Head rectangular, not narrowing anteriorly or posteriorly; prosternum without denticles …. 12
12. Pronotum wide, width to length ratio 1.8–2; 25–30 cells in one elytral row 13
– Pronotum less wide, width to length ratio 1.2–1.3; 20–25 cells in one elytral row ……..... 14
13. Large beetles, body length more than 20 mm. Elytral cells medium-sized, about 25 cells in one elytral row. Epipleuron wide, strongly and abruptly narrowing at basal third. Metaventrite`s width 1.8 times exceeds length. Length of apical abdominal sternite two times as long as wide .... ***N. diazromerali***
– Beetle less than 10 mm in length. Elytral cells small, about 30 cells in one elytral row. Epipleuron narrow, gradually narrowing at basal half. Metaventrite`s width and length are equal. Width of apical abdominal sternite 1.4 less its length .... ***N. pingi***
14. Apical abdominal sternite to penultimate one length ratio more than three (Fig. 60) .... …………………………………..…………………………………….….. ***N. lapidarius***
– Apical abdominal sternite to penultimate one length ratio 2.3–2.8 15
15. Cuticular tubercles not larger than 0.03 mm, density no less than 760 tb/mm^2. Epipleuron narrow, weakly and gradually narrowing at elytron basal third (Fig. 7) .... ……………………………………………………………………………….… ***N. picturatus***
– Larger tubercles: 0.03–0.05 mm in diameter, density no more than 320 tb/mm^2. Epipleuron of medium width, abruptly narrowing at elytron basal third (Figs 27, 28) .... ***N. elegans***

Genus *Brachilatus* Strelnikova et Yan, gen. n.

https://zoobank.org/NomenclaturalActs/FDC38409-9395-4F53-88B2-D5CD0A78494C

Type species: *Notocupes nigrimonticola* Ponomarenko, 1968; here designated.

DIAGNOSIS. Beetles with wide bodies, length to width ratio 1.8–2.1. Antennae filiform or weakly serrated. Pronotum rounded, narrowing anteriorly and posteriorly, anterior angles strongly protruding forward and reach base of compound eyes or goes beyond it. Pronotum and elytron wide; elytron 1.3–1.7 times wider than pronotum. Sides of pronotum and elytral epipleural margin could be dentate along entire length. Epipleural margins of elytron straight at basal half, then gradually curving towards body midlength; humeral bulges distinct, protruding laterally. Epipleuron 4.3–6.2 times narrower than elytron, almost not narrowing or abruptly narrowing at base. Veins 2 and 3 not merging before reaching elytral apex.

COMPOSITION. Nine species from Jurassic of Germany and Kazakhstan, Lower Cretaceous of Spain, Mongolia, South Korea and Upper Cretaceous of Kazakhstan. All species are here transferred from *Notocupes* to new genus and nine new combinations are proposed: *Brachilatus nigrimonticola* (Ponomarenko, 1968), **comb. n.**; *B. caducus* (Ponomarenko, 1969), **comb. n.**; *B. dundulaensis* (Ponomarenko, 1994), **comb. n.**; *B. foerstery* (Ponomarenko, 1968), **comb. n.**; *B. longicoxa* (Soriano et Martinez-Delclòs, 2006), **comb. n.**; *B. oculatus* (Soriano et Martinez-Delclòs, 2006), **comb. n.**; *B. premeris* (Lee et al., 2022), **comb. n.**; *B. spinosus* (Li et Cai, 2023), **comb. n.**; *B. viridis* (Soriano et Martinez-Delclòs, 2006), **comb. n.**

ETYMOLOGY. From Latin "brachi" – shoulder and "latus" – broad.

Key to species of the genus *Brachilatus*

1. Elytron and pronotum has denticles; 25 of elytral cells in one row; apical abdominal sternite have rounded apex, 2.5 times longer than penultimate one 2
– Elytron and pronotum has no denticles; 21–30 of elytral cells in one row; apical abdominal sternite has rounded or acute apex, 1.7–3.1 times longer than penultimate one 3
2. Epipleural margin dentate along its entire length .... ***B. viridis***
– Epipleural margin dentate only at humerus level .... ***B. caducus***
3. About 30 cells in one elytral row 4
– Only 21–25 cells in one elytral row 5
4. Paracoxal suture does not reach metaventrite posterior angles; apical abdominal sternite 2.6 times longer than penultimate one .... ***B. premeris***
– Paracoxal suture does not reach metaventrite posterior angles; apical abdominal sternite 2 times longer than penultimate one .... ***B. dundulaensis***
5. Eyes small, their transverse diameter is more than 5 times the head width. Epipleuron 4.4–4.9 times shorter than elytron 6
– Eyes large, their transverse diameter 3.3–3.8 times shorter than head width. Epipleuron 4.3 or 5.5–5.8 times shorter than elytron 7
6. Head wide, 1.6 times narrower than pronotum .... ***B. oculatus***
– Head narrow, 2.3 times narrower than pronotum . ... ***B. foerstery***
7. Epipleuron 4.3 times narrower than elytra. Apical abdominal sternite to penultimate one length ratio is 3.1 .... ***B. spinosus***
– Epipleuron 5.5–5.8 times narrower than elytra. Apical abdominal sternite to penultimate one length ratio is 2.4–2.6 8
8. Body elongated, length to width ratio 2.1. Head narrow, pronotal width to head width ratio 5. Epipleuron almost does not narrow towards the apex. About 21 cells in one elytral row .... ***B. nigrimonticola***
– Body broad, length to width ratio 1.8. Head narrow, pronotal width to head width ratio 1.9. Epipleuron sharply narrows in the anterior part. About 25 cells in the elytral row (Fig. 8) .... ***B. longicoxa***

Genus *Zygadenia* Handlirsch, 1906

Zygadenia Handlirsch, 1906: 558 (type species: *Curculionites tuberculatus* Giebel, 1856); Jarzembowski, 1993: 179; Ponomarenko, 2000: 317.

Kakoselia Handlirsch, 1906: 561 (type species: *Camptodontus angliae* Brodie, 1845); Ponomarenko, 2006: 95.

Type species: *Zygadenia tuberculata* (Giebel, 1856).

DIAGNOSIS. Elytron from 4 to 14 mm long, bear four veins, a scutellar striole and an outer sulcus along epipleural margin; there are double rows of cells between veins. Veins 2 and 3 often have a common base, could merge before reaching elytral apex; veins 4 and 5 always merging before reaching elytral apex (Figs. 2–4). Humerus (humeral bulge) not protruding anterolaterally, rounded. Epipleural margin gradually curving; elytral apex blunt. Epipleuron usually wide (only in *Z. simpsoni* and *Z. angliae* narrow), often narrowing at elytral base (only in *Z. sinitsae* and *Z. semen* almost not narrowing).

REMARKS. The genus *Zygadenia* composed purely of the species described on the basis of isolated elytron (importance of having such taxon is discussed in Strelnikova & Yan, 2023).

COMPOSITION. There are 12 species from Lower Jurassic of Australia, Upper Jurassic of Germany and Mongolia, Lower Cretaceous of China, England and Russia, namely *Z. tuberculata* (Giebel, 1856) [*Innominatus tuberculatus* Brodie, 1845; *Curculionites tuberculatus* Giebel, 1856], *Z. alexrasnitsyni* Strelnikova et Yan, 2021, *Z. angliae* (Giebel, 1856) [*Camptodonthus angliae* Brodie, 1845; *Kakoselia angliae* Handlirsch, 1906], *Z. floodpagei* Jarzembowski et al., 2015, *Z. giebeli* Ponomarenko, 2014, *Z. handlirshi* Ponomarenko, 2014, *Z. liui* Jarzembowski et al., 2015, *Z. semen* Ponomarenko, 2000 [*Notocupes*], *Z. sibirica* Ponomarenko, 2000 [*Notocupes*], *Z. simpsoni* Jarzembowski et al., 2015, *Z. sinitzae* Ponomarenko, 2000, *Z. westraliensis* Riek, 1968 [*Mesothoris*].

Indeterminate species of *Zygadenia* were reported from the Middle Triassic of Switzerland, the Lower Jurassic of Australia, the Lower Cretaceous of England and the Upper Cretaceous of Argentina.

Key to species of the genus *Zygadenia*

1. Elytron distinctly shorter than 9 mm, elytral cells small 2
– Elytron at least 9 mm long, cells of different sizes 4
2. Elytron 4–5 mm long; about 25 cells in one elytral row; epipleuron narrow with no cells on it .... ***Z. angliae***
– Elytron 6.8–8.9 mm long; 28–30 cells in one elytral row; epipleuron wide at base, then narrows abruptly, with full row of cells 3
3. Epipleuron with large row of cells the same size as on disk; 28 cells in one elytral cell row on elytron\`s disc .... ***Z. sibirica***
– Epipleuron with narrow row of cells, smaller and fainter than on disk; 30 cells in one elytral cell row on elytron\`s disc .... ***Z. westraliensis***
4. Elytron about 14 mm long, strongly elongated, length to width ratio 3.7; 31 small cells in one elytral cell row .... ***Z. simpsoni***
– Elytron about 9–16.5 mm long, less elongated, length to width ratio 2.4–3.2; 20–38 small cells in one elytral cell row 5
5. Elytron wide, length to width ratio 2.4–2.6 .... ***Z. floodpagei***
– Elytron slightly narrower, length to width ratio 2.8–3.2 6

6. In one elytral row 38 cells (Figs 25, 26) .... ***Z. alexrasnitsyni***
– In one elytral row 20–25 cells 7
7. In one elytral row 20 large cells 8
– In one elytral row 24–25 smaller cells 10
8. Elytron 9 mm long .... ***Z. handlirshi***
– Elytron 10–13 mm long 9
9. Elytral length to width ratio 2.9 .... ***Z. giebeli***
– Elytral length to width ratio 3–3.2 .... ***Z. tuberculata***
10. Elytral cells small; epipleuron abruptly narrowing at distal half .... ***Z. liui***
– Elytral cells medium-sized or large; epipleuron almost not narrowing towards elytrons apex 11
11. Elytron 14–15.5 mm long, elytrons length to width ratio 2.8–3, elytral cells large .... ***Z. sinitzae***
– Elytron 10.9–12.4 mm long, elytrons length to width ratio 3.1–3.2 elytral cells medium-sized .... ***Z. semen***

Odontomma patula **(Ponomarenko, 1985), comb. n.**
Figs 9–12

Notocupes patulus Ponomarenko, 1985: 48, tab.VI, fig. 1.

MATERIAL EXAMINED. Holotype, PIN no. 4034/2 – print and counterprint of elytron, metaventrite, and abdomen, apices of elytron and abdomen not preserved; Layma locality, Tyumen Formation, Middle Jurassic.

DIAGNOSIS. Abdomen covered with large, sparse tubercles, density 175 tb/mm^2. Elytron has up to around 38 small cells in the row.

DESCRIPTION. Epipleuron wide, gradually curving along its length, weakly narrowing at basal half to about 1/3 of its original width. Elytral base straight; humeral bulge distinct, rounded. Elytral cells small, more than 30 cells in a single row. Metaventrite trapezoid, his width 2.5 times exceeds length. Paracoxal suture do not reaches posterior angles of metaventrite. Central portion of abdominal sternites covered with large tubercles (0.05–0.07 mm in diameter; 0.02–0.06 distance between tubercles). Metacoxae strongly transverse, width two times exceeds length, covering half of first visible abdominal sternite.

MESUREMENS. Approximate body length 13, length of preserved body part 8.7, approximate elytral length 10, width at basal third 4.

COMPARISION. Similar to *Odontomma trachylaena* Ren et al., 2006 and *O. sulcatum* (Tan et al., 2007) in having small elytral cells and paracoxal suture not reaching posterior margins of metaventrite. Differs from *O. trachylaena* in noticeably smaller size and from *O. sulcatum* in smaller density of cuticular tubercles, and from both species in narrower epipleuron.

REMARKS. This species cannot be assigned to any of the five genera previously comprised former *Notocupes*. Here it is transferred from *Notocupes* to *Odontomma* Ren et al., 2006 on the basis of follow features: body covered with large, sparse tubercles; elytral base straight, humeral bulge distinct; epipleural margin dentate along its length; rather wide, only weakly narrowing posteriorly, epipleuron. There are no species with posteriorly widening epipleuron, if epipleuron is wide near elytral base it is usually strongly narrowing at the elytron midlength (Figs 4, 25–28).

DISCUSSION

For species identification in such a large group as *Notocupes* in its former composition, relative characters, such as elytral or head length, “large/medium/small”, or “wide/narrow” *etc.* have limited usefulness. In the table of morphological characters (see above) and new descriptions, such features were replaced with comparative lengths of corresponding body parts. For example, eye size in different species could be compared with head width to eye ratio; epipleuron width – with elytral width to epipleuron width at base ratio *etc*.

Special attention should be payed to cuticle: tubercles on integuments, previously not considered as a character, appeared to have three size categories: from small ones (up to 0.02 mm in diameter), to medium-sized (0.02–0.04) and large (0.04–0.07 mm in diameter). This character could be applied to separate genera and to show some evolutionary tendencies (Strelnikova & Yan, 2023). Analysis of integument sclerotization reveals, that older taxa, found in the Triassic and the Early Jurassic localities were covered with tubercles of single type not exceeding 0.04 mm in diameter, only *Rh. cellulosus* (Issyk-Kul, Early Jurassic) possess two different types of tubercles. The Middle to Late Jurassic and Cretaceous species usually covered with tubercles of two types, which are generally larger than 0.04 mm. Single studied the Late Cretaceous *B. caducus*, have three types of tubercles (Fig. 31), as extant Archostemata do. There is an evolutionary tendency for younger species to have two types of tubercles (Fig. 13).

Head protuberances, previously reported only for a few selected species, were described for all species from PIN RAS collections. Lack of information about this character in other species make it too early to draw a major taxonomic conclusion but could be quite useful as previously mentioned cuticular sculpture.

Bodies of *Distocupes varians* (Lea, 1902) (Cupedidae) and *Omma stanleyi* Newman, 1839 (Ommatidae) have tubercles of three types, as in the Late Cretaceous *B. caducus.* However, their localization is different for extant modern species and *Brachilatus.* Large tubercles located along the anterior margin of sternites and in its median part. Middle-sized tubercles lie along sternite`s posterior margin and separate areas with large tubercles as a thin divider. Small tubercles cover triangle-shaped areas on both sides of sternite, as in *N. excellens* or *N. caudatus* (Figs 14, 21). Body of *Priacma serrata* (LeConte, 1861) (Cupedidae) is different from aforementioned *Distocupes* and *Omma*, because it is covered with just two types of tubercles, small tubercles cover only posterior part of sternites.

Bodies of extant Archostemata often covered with scales of different shapes depending on the size of tubercles to which they are attached to. Large tubercle typically bears broad scales (Figs 17, 19, 23), middle-sized tubercles as in *Distocupes* and *Omma* bears more elongated scales (Fig. 20), small tubercles of *Priacma* have thin, setae-like scales (Fig. 18).

It is possible to assume, that similar distribution of different scales on tubercles of different sizes might be true for fossils of *Notocupes*-related genera. Presence of small punctures on the top of tubercles in the Triassic *Rhabdocupes* could indicate elongated, maybe even setae-like integuments as in *Priacma* (Strelnikova & Yan, 2023, fig. 7b; Fig. 18). This structure of integument of Triassic and some Jurassic species can be considered more archaic. The Jurassic and Cretaceous species of *Notocupes* and *Brachilatus*, covered with two types of tubercles, large and small, probably bore wider scales like *Omma* or *Distocupes* and this type of integument is more advance. Moreover, the Triassic *Rhabdocupes* has a tiny hole in the middle of the tubercles which can be identified as the place for scales attachment similarly to modern *Priacma* (Strelnikova & Yan, 2023, fig. 7b; Figs 17, 18). The scales of *Distocupes* and *Omma* are attached to the posterior part of the tubercle (Figs 19, 20, 23). There are holes on the inside of sternites (Fig. 22).

Cuticular tubercles could be used to separate different genera from the previously single *Notocupes*. For example, all studied species of *Conexicoxa* are covered by tubercles of single type not larger than 0.04 mm in diameter; *Odontomma* is only covered by large tubercles; *Brachilatus* bears two types of tubercles, or, rarely three; *Rhabdocupes* covered by tubercles of single type, except *Rh. cellulosus* (Fig. 24). This could potentially be used to identify strongly damaged or incomplete specimens.

Present study allowed to define characters, applicable to most species previously assigned to *Notocupes*. As an example of a character with limited diagnostic usefulness of a prosternal intercoxal process could be mentioned. This process is often visible on material from China and Myanmar and was mentioned as diagnostic feature from *Ovatocupes* and *Amblomma* (Tan & Ren, 2006, figs 1–4; Li *et al*., 2023a, fig. 3; Li *et al*., 2023b, figs 9–12), but within PIN RAS collections could only be seen on *Rh. laticella* (Strelnikova & Yan, 2023, fig. 2). Prosternal intercoxal process cannot be preserved on the prints or cannot be visible due to the poorer preservation of prints from PIN.

Previously it was stated, that it is impossible to define a general venation pattern for *Notocupes* and published ones are contradicting each other (Kirejtshuk, 2020; Strelnikova & Yan, 2021, 2023). However, studying this character on PIN RAS material showed venation of two types: 1) veins 2 and 3 are reaching elytral apex, veins 4 and 5 merging before reaching elytral apex (Figs 25, 26); 2) pairs of veins 2,3 and 4,5 are merging before reaching elytral apex (Figs 27, 28). Second type of venation has been found only in species of *Conexicoxa* (found in all species except one, where this character is unclear, Fig. 24) and *Notocupes*. It is not always clear where veins 2 and 3 are merging, since that portion of elytron is bending, thus veins are often overlapping each other on the imprint. This character could be used as additional criteria to separate genera.

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